

ART. VII.—*On the Displacement of the Optic Lobes during the Development of the Brain of the Fowl.*

By K. K. OLIVER

(Government Research Scholar, Biological Department, University of Melbourne).

(With Plates XXV.—XXXV.).

[Read 13th July, 1911].

In the following paper a series of drawings is presented which endeavours to illustrate clearly the manner in which the optic lobes of the common fowl, *Gallus domesticus*, form and change their position. The earliest drawing shows the mesencephalon as a single median structure on the dorsal surface, and the subsequent ones, its division into a bi-lobed structure, and its displacement caused by the development and growth both of the lobes themselves and of the adjacent parts. The later-stage drawings depict the lateral and ventral course of the optic lobes and their final attainment of the adult latero-ventral position. No attempts at histological work have been made, the morphological relationships alone having been considered.

The search through a very large number of memoirs dealing with the development of the brain has shown that the literature on this subject is concerned almost entirely with histological work, and I have been able to find very few references to the particular aspect of the work with which this paper deals.

A. Milnes Marshall in his "Vertebrate Embryology," p. 256, mentions the fact that the mesencephalon, till the end of the 4th day of incubation, remains approximately spherical, and on the 5th the optic lobes begin to form; also that on the 16th day the optic lobes begin to become pushed apart, and take up their adult position.

Frank R. Lillie, in "The Development of the Chick," mentions the formation of the optic lobes, but in connection with a detailed account of the rest of the brain only. A consecutive

series of drawings, depicting the external formation and the descent of the optic lobes in relation to the adjacent parts of the brain, has apparently not been taken before—hence the present paper.

The drawings are divided into 10 sets of 6 each, and an eleventh set, showing the dorsal and lateral view of the adult brain for comparison with the foregoing figures. Each of the ten sets contains two solid drawings, that of the dorsal and lateral views respectively. There are also three sections taken transversely across the optic lobes—(1) across the anterior portion, (2) across the middle, and (3) across the posterior portion. The sixth drawing is a diagram of the lateral view of the brain, showing the approximate direction of the above three sections.

The solid drawings are taken under the camera lucida, and are as nearly as possible twice their real size. The sections are drawn under a Leitz camera lucida, and $1\times$ power, Leitz lens, and have been halved in reproduction.

The work has been carried on in the Biological Laboratory of the Melbourne University, and I should like to express my thanks to Professor Baldwin Spencer for assistance and advice, and to Messrs. J. Brake, A. O. V. Tymms and A. L. Rossiter for help in various ways.

Stage I. (Pl. XXV.)

The first stage corresponds approximately with the period of four days' incubation. At this point of development, the mesencephalon is represented by a very marked median dorsal swelling, which is usually said to correspond to the fourth and fifth neuromeres. A very slight groove (1b) beginning to form in the sagittal plane, and extending right along the dorsal surface of the mesencephalon, is the first indication of the division into the optic lobes. The epiphysis at this time is becoming prominent, and the cerebral hemispheres have assumed the dorsally recurved appearance characteristic of their earlier development.

In 1a, a lateral view of the brain is shown, with the eye forming. The epiphysis is seen in profile. The great distance between the small cerebral hemispheres, and the large mesence-

phalon is worth remark. Between the mesencephalon and metencephalon the isthmus is very distinctly marked. At this stage the line of axis of the mesencephalon and the metencephalon, and the line of axis of the cerebral hemispheres and the mesencephalon form an acute angle.

1c (Fig. 1, Section 1) shows a transverse section through the anterior portion of the mesencephalon. The walls of the mesencephalon are thin, and the lumen of the cranial cavity great in comparison with the thickness of the cranial wall.

1d (Fig. 1, Section 2) shows a transverse section through the centre of the mesencephalon and metencephalon. The section owes its apparently continuous shape to the fact that, because of the flexure of the brain, the section through the mesencephalon is transverse, and that through the metencephalon longitudinal.

1e (Fig. 1, Section 3) shows the posterior portion of the mesencephalon. The slight groove marking the beginning of the optic lobes is faintly indicated.

Stage II. (Pl. XXVI).

This stage corresponds approximately with the period of five days' incubation. At this stage the mesencephalon has become very definitely divided in the sagittal plane, the groove shown in stage I. having deepened in such a way as to indicate the outlines of the optic lobes. Although further development has taken place, these have not increased in size as much as the cerebral hemispheres, which are now assuming a definite form, and are enlarging considerably. This growth brings the cerebral hemispheres further back, towards the optic lobes, but there is a distinct space still between them.

The dorsal view (2b) shows the clear division of the mesencephalon into the two optic lobes, so that now, from being single and median, the mesencephalon has become a paired lateral structure, which is still very prominent on the dorsal surface. The cerebral hemispheres have increased in size at a rate which is out of proportion to the rate of growth of the optic lobes, which, though undergoing further development, have not materially enlarged since the preceding stage. The epiphysis is still

well marked, though the diencephalon is now becoming relatively smaller than either the telencephalon or the mesencephalon. The first traces of the future cerebellum are not visible from the dorsal aspect, the swelling of the optic lobes posteriorly preventing this.

In the lateral view (2a) the rounded, more or less definite form of the cerebral hemispheres is seen beginning to encroach on the diencephalon from the anterior end, while at the same time the optic lobes are beginning to overgrow it from the posterior. The epiphysis is very definite on the dorsal surface, and the optic chiasm infundibulum are beginning to appear ventrally. The metencephalon, showing traces of the upwards and outwards growth which later form the cerebellum, is visible below the optic lobes. The angle formed by the axes of the telencephalon, diencephalon and mesencephalon, and of the mesencephalon, metencephalon and myelencephalon, is still rather less than a right angle, but is not so acute as in stage I.

2c (Fig. 2, Section 1) is a transverse section across the anterior part of the optic lobes. The lobes are now seen to be lateral in position, and the walls are becoming slightly thicker, while the optocoele is beginning to become smaller.

In 2d (Fig. 2, Section 2) a section is taken across the middle of the optic lobes, the cranial flexure still being so great as to cause the metencephalon and myelencephalon to appear as a longitudinal section.

2e (Fig. 2, Section 3) cuts through the posterior portion of the optic lobes, and the first beginnings of the cerebellum.

Stage III. (Pl. XXVII.)

The third stage corresponds approximately to a period of nine days' incubation. The mesencephalon is now divided into two rounded, dorso-laterally placed structures, which are from this time on called the optic lobes. They are still very large, comparatively, and form the most prominent portion of the brain. By this time the shape of the cerebral hemispheres has become quite definite and characteristic, and the olfactory nerve has begun to become apparent at the anterior end.

In 3b the cerebral hemispheres can be seen to be becoming elongated, and are stretching backward to meet the forward growing optic lobes. The epiphysis is prominent in the space still existing between the two pairs of structures, which is all that is visible of the diencephalon from the dorsal aspect. The forming cerebellum is hidden by the backward growth of the optic lobes.

In 3a the approximation of the cerebral hemispheres to the optic lobes is very marked in comparison with the preceding stage. From the lateral position the only part of the diencephalon visible is the epiphysis on the dorsal, and the infundibulum and optic chiasma on the ventral surface. The ventrolateral depression, caused by their position against the back of the orbit, is now becoming visible in the cerebral hemispheres, and the olfactory nerve is also to be seen forming. The optic lobes have grown forward in such a way as to overshadow the diencephalon from behind and the metencephalon from above. The lateral enlargement of the metencephalon, marking the commencement of the cerebellum, is becoming more clearly indicated.

3c is a transverse section in the plane indicated in Fig. 3, Section 1. It shows the increase of the brain substance over the preceding stage, and the thickening of the walls of the optic lobes.

In 3d the lateral position of the optic lobes is very definite. The crura cerebri are faintly indicated at this stage.

3e is a transverse section across the hinder part of the optic lobes, and just touches the myelencephalon longitudinally.

The axis of the cerebral hemispheres and the optic lobes, and that of the optic lobes and the metencephalon and myelencephalon have now altered, so as to become approximately at right angles to one another.

Stage IV. (Pl. XXVIII.)

The fourth stage corresponds approximately with a period of 10 days' incubation. In the dorsal view (4b) the cerebral hemispheres can be seen as elongated, closely opposed structures. Laterally they have encroached on the diencephalon in

such a way as to hide it except at the median dorsal surface. The epiphysis is distinctly visible in the centre of this space. The optic lobes have encroached on the diencephalon, so that now they are closely approximated to the cerebral hemispheres. The pressure between the two portions of the brain is such that the optic lobes are beginning to be pushed out laterally, and their axis in the longitudinal vertical plane tends to become placed obliquely to that of the cerebral hemispheres and diencephalon in the same plane. The outgrowth of the metencephalon, to form the cerebellum, is now becoming visible between the posterior portions of the optic lobes.

In 4a the backward growth of the cerebral hemispheres and the forward growth of the optic lobes, so as to be in close approximation with each other, is clearly indicated. The optic chiasma and the infundibulum are distinct, and the ventrolateral depression of the cerebral hemispheres, caused by the formation of the floor of the orbit, is becoming more clearly marked. The epiphysis, still comparatively large, is seen in profile. The rotation of the axis of the optic lobes is not so easily discernible in the lateral view. The fold of the metencephalon, destined to become the cerebellum, is assuming a more definite shape, and the angle formed by the axis of the cerebral hemispheres and the optic lobes in longitudinal horizontal plane, and the axis of the optic lobes, and metencephalon, and myelencephalon in the same plane, is becoming much more obtuse, it now being somewhat less than a right angle.

4c (Fig. 1, Section 1) is taken across the anterior part of the optic lobes, and includes the epiphysis on the dorsal surface, and the metencephalon and myelencephalon in the longitudinal section.

The walls of the optic lobes are becoming much thicker now, and the histological structure is commencing to be differentiated.

4d (Fig. 4, Section 2) is a section across the centre of the optic lobes.

The crura cerebri are more definite than in the preceding figures, and the myelencephalon is seen in longitudinal section.

4e (Fig. 4, Section 3) shows the posterior portion of the optic lobes in section. They are thicker-walled than in the preceding stage, and their histological structure is more definite.

Stage V. (Pl. XXIX.)

The fifth stage corresponds approximately to a period of twelve days' incubation.

On viewing the specimen dorsally (5b) marked changes will be seen to have taken place since the last stage. The anterior portions of the cerebral hemispheres are now more closely opposed to each other than are the posterior parts. The optic lobes are becoming so rotated that their longitudinal vertical axes are almost at right angles to the axis of the cerebral hemispheres. The cerebral hemispheres are beginning to rise up dorsally, so that they overshadow the diencephalon and the epiphysis somewhat, and the pressure exerted on the optic lobes by them is beginning to force the optic lobes apart. Dorsally, the optic lobes are still prominent, but not so much so as at the preceding stages. So far it has been rather that the surrounding parts have grown up to the level of the optic lobes, than that they themselves have grown down, but from this stage on, the optic lobes descend steadily, presumably owing to the pressure brought to bear on them anteriorly by the cerebral hemispheres first, and then, later, posteriorly by the dorsal development of the cerebellum. The cerebellum at this stage has become distinctly indicated, and is beginning to assume its typical convoluted appearance. The dorso-lateral growth of the metencephalon has increased in such a manner as to begin to curl over on itself towards the myelencephalon, while on the dorsal surface of this area there are some six faintly marked convolutions appearing. The myelencephalon at this stage is also beginning to assume the characteristic appearance of the medulla oblongata, and both cerebellum and medulla are clearly seen from the dorsal aspect, the cranial flexure having changed so that the axes of fore, mid and hind brain now lie along approximately the same straight line.

The lateral view (5a) shows a distinct change in shape. The diencephalon is now completely hidden by the pushing out of the optic lobes to the sides. The change in the direction of the axes of the lobes is much more clearly seen at this stage than at the preceding one. The epiphysis is hidden by the growth of

the cerebral hemispheres on either side, and the optic chiasma and infundibulum are less distinct. The ventro-lateral depressions of the cerebral hemispheres are at this stage very distinct, there being a hemispherical concavity on each side of this portion of the brain. The characteristic backwards curling cerebellum, with its faintly marked convolutions, is a marked feature of this stage, and the long axes of the fore, mid and hind brain now lie in the same general direction.

In 5c (Fig. 5, Section 1) the increase of amount of the brain substance is worthy of remark. The section is purely transverse now, the change in the direction of the axis of the medulla eliminating the necessity of cutting it longitudinally.

5d (Fig. 5, Section 2) shows the lobes at about the centre. The *crura cerebri* are very distinct now, and are beginning to fill a considerable portion of the cavity of the optocoel.

A section across the posterior portion of the lobes in 5e (Fig. 5, Section 3) shows the increased thickness of the walls at this stage.

Stage VI. (Pl. XXX.)

The sixth stage corresponds approximately to the period of thirteen days' incubation.

The dorsal view shows little change since the last stage. The cerebral hemispheres are becoming rather fuller and more rounded in appearance, and are now well developed on the dorsal surface. The epiphysis is distinct in the space between the cerebral hemispheres and the optic lobes. The optic lobes themselves are beginning to become more decidedly flattened antero-dorsally, and have the appearance of being squeezed between the cerebral hemispheres and the cerebellum in such a way as to force the lobes down to a lateral and ventral position, so that the greatest breadth of the brain is now that across the optic lobes, and their long axis is at right angles to that of the cerebral hemispheres and the cerebellum. The cerebellum has developed considerably, and is now definitely convoluted, and the flocculi are commencing to be formed laterally. The myelencephalon has assumed the definite form of the medulla oblongata.

In the lateral view (6a) the curved surface of the cerebral hemispheres can be seen to have become more prominent dorsally than the optic lobes, which are now so far pushed laterally and ventrally that the chiasma and infundibulum are scarcely seen. The lobes have assumed a definite oval shape at this stage. The cerebellum has developed considerably, there now being eight convolutions visible from the lateral aspect. The flocculi, too, are taking definite form, while the medulla has increased in size, and is in proportion to the rest of the brain.

6c (Fig. 6, Section 1) shows the most anterior portion of the optic lobes, but so far forward that there is no optocoele included, and ventrally the chiasma has been cut through.

In 6d (Fig. 6, Section 2) a section about the centre of the lobes is given, showing the connection of the optocoele with the other brain cavities.

6e (Fig. 6, Section 3) cuts through the posterior portion of the optic lobes and the anterior convolution of the cerebellum.

Stage VII. (Plate XXXI.)

The seventh stage corresponds approximately to a period of 14 days' incubation.

In dorsal aspect the cerebral hemispheres are seen to have become roughly triangular, and are increasing in size at a proportionately greater rate than the optic lobes (7b). The epiphysis is now closely surrounded by the cerebral hemispheres anteriorly, and the optic lobes posteriorly. The optic lobes have quite lost their dorsal prominence, and are now lateral structures. The cerebellum has increased greatly both in size and in the definite formation of its convolutions, there being now eight definite convolutions visible on the dorsal aspect. The ninth, and originally the most posterior convolution, is hidden underneath the one anterior to it, in earlier development, though now, through the curling back of the cerebellum, posteriorly placed. The medulla is much as in the last stage, but the development of the cerebellum has partially hidden it.

In 7a the cerebral hemispheres can be seen to be becoming more developed. The ventro-lateral depressions are clearly marked. The optic lobes have altered but little since the pre-

ceding stage; they have sunk slightly towards the ventral surface. The cerebellum has become enlarged, and is now the most prominent feature of the brain dorsally. Nine convolutions are visible from this view, and the flocculi are becoming distinctly marked. The medulla remains much as at stage VI.

7c (Fig. 7, Section 1) is taken from the most anterior portion of the optic lobes. On the dorsal surface the epiphysis is cut through, and on the ventral the optic chiasma is seen. The walls of the lobes only are seen, for the section is anterior to the optocoele.

7d (Fig. 7, Section 2) shows a section at about the centre of the lobes. The brain substance is rapidly increasing in such a manner as to tend to fill the cavity of the optic lobes, so that the optocoele is now becoming much diminished in size. The crura cerebri are well developed.

In 7e (Fig. 7, Section 3) the posterior portion of the optic lobes, with the posterior portion of the optocoele, is seen. The cerebellum has assumed a very characteristic and definite shape and position by this time.

Stage VIII. Pl. XXXII.)

The eighth stage corresponds approximately to a period of 16 days' incubation.

In the dorsal view the cerebral hemispheres are seen to have become more triangular in shape than in the preceding stage. The cerebellum is growing forward so as to reach the posterior region of the cerebral hemispheres, and is overshadowing the epiphysis posteriorly, while the quickly enlarging cerebral hemispheres are beginning to hide it somewhat anteriorly. Eight distinct convolutions can be seen in the cerebellum at this stage, and the flocculi are becoming steadily more definite. The optic lobes are now most distinctly becoming overgrown and pushed down by the cerebral hemispheres and cerebellum, and are moving out and down to their final ventro-lateral position. The medulla is much as in the preceding stage.

The lateral view (8a) shows how very prominent the cerebellum has by this time become. Nine distinct convolutions are visible, and the flocculi are more distinct. The cerebral

hemispheres are now above the optic lobes on the dorsal surface, and the optic lobes are moving down in a more or less directly dorso-ventral line. The ventro-lateral depressions of the cerebral hemispheres are becoming somewhat less distinct. The medulla is much the same as in stage VIII.

8c (Fig. 8, Section 3) is taken across the most anterior part of the optic lobes, the cavity of which is seen to be fast becoming filled by the growth of the brain substance composing its walls. The anterior lobe of the cerebellum can be seen in the median line, having by this time grown forwards and upwards until it is most prominent dorsally.

8d (Fig. 8, Section 2) shows a section across the middle of the optic lobes. The cerebellum can be seen to have assumed a prominent dorsal position in the sagittal plane. The optic lobes are sinking lower.

8e (Fig. 8, Section 1) is a section across the posterior part of the optic lobes, at the spot where the optocoele is almost obliterated. The cerebellum is beginning to assume its relatively large adult size.

Stage IX. (Pl. XXXIII.)

The ninth stage corresponds approximately to a period of eighteen days' incubation.

Dorsally there is very little change from the preceding stage to be seen. The cerebral hemispheres have increased slightly in size, and overhang the optic lobes on the dorsal surface rather more than in the previous stage. The cerebellum is enlarging still, and now shows nine convolutions from this view; the flocculi have become definitely established, and are now a characteristic feature of the brain. The epiphysis is comparatively insignificant in size, though a distinct structure. The most anterior portion of the cerebellum has grown forward in such a way as to meet the posterior portions of the cerebral hemispheres, and the optic lobes are clearly seen to have become pushed out laterally, and pressed down ventrally.

In the lateral view the optic lobes will be seen to have descended considerably; they are moving forward ventrally as well as downwards. The cerebellum is well developed on the

dorsal surface, and is approximated to the cerebral hemispheres, which are still growing back posteriorly. Ten convolutions are apparent in the lateral view. The ventro-lateral depressions of the cerebral hemispheres are becoming less marked. The medulla is much as at the preceding stage.

9c (Fig. 9, Section 1) is taken across the anterior portion of the optic lobes in such a way as to show the optocoele, now rendered crescent-shaped and much smaller by the great increase in the brain substance. Above the optic lobes is seen the hinder portion of the cerebral hemispheres, now growing over the optic lobes from before back, and tending to hide them from view dorsally. The epiphysis is visible in the mid-dorsal line of this figure.

9d (Fig. 9, Section 2) is a section across the centre of the region of the optic lobes. It shows a marked increase in the size of the cerebellum, together with the decidedly lateral position now assumed by the optic lobes.

9e (Fig. 9, Section 3) is a cut across the posterior part of the region of the optic lobes. It shows the most posterior portion of the optic lobes, the cavity of which is not seen, the section being taken so far back as to cut through the brain substance only. The cerebellum is very definite in the mid-dorsal line, and has assumed almost adult proportions,

Stage X. (Pl. XXXIV.)

The tenth stage corresponds approximately with a period of 20 days' incubation.

In the dorsal aspect (10b) there will be seen a marked difference in the size of the brain. The cerebral hemispheres are overshadowing the optic lobes very markedly from the anterior, and the cerebellum is also growing over them from the middle outwards. The optic lobes can now scarcely be called latero-dorsal structures, but rather latero-ventral. In the cerebellum nine well-developed convolutions are visible, and the flocculi are well marked. The epiphysis, though still present, is now but faintly seen, and is sunk in between the posterior portions of the cerebral hemispheres and the anterior part of the cerebellum.

Laterally (10a) the cerebral hemispheres are seen clearly to be growing over the optic lobes, from the anterior posteriorly, and from the dorsal surface ventrally. The approximation of the cerebellum and the cerebral hemispheres has squeezed the optic lobes in such a manner as to cause their greatest development to take place ventrally, so that now the structures can be seen to have become definitely ventro-lateral. The cerebellum has eleven convolutions visible in this view, and the flocculi have assumed the characteristic appearance found in the hatched bird. The ventro-lateral depressions of the cerebral hemispheres have become so faint as to be scarcely visible. The medulla is much the same as in the previous stage.

10c (Fig. 10, Section 1) shows a cut through the fore part of the optic lobes, at the place at which the optocoele extends furthest anteriorly. The chiasma is indicated ventrally, and the most anterior convolutions of the cerebellum are shown. Dorsal to the optic lobes in this section, the most posterior portions of the cerebral hemispheres appear, so relegating the optic lobes to a very definitely ventro-lateral position.

In 10d (Fig. 10, Section 2) a section across the middle of the optic lobes is given. The cerebellum is distinct in the centre dorsally, and the optic lobes themselves are seen in a ventral and lateral position. The optocoele is now to a great extent obliterated by the great increase in size of the crura cerebri, and assumes a roughly hemispherical shape in transverse section.

In 10e (Fig. 10, Section 3), the enormous development of the cerebellum is visible, taking up practically all the dorsal surface in the section, and the optic lobes are most distinctly seen to be lateral and ventral in position; the optocoele is not seen at all in this section.

The Adult Brain. (Pl. XXXV.)

The adult brain is inserted merely for comparison. I have not worked it at all, so can give no description of it.

